A STUDY OF HYBRIDS IN EGYPTIAN COTTON

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Introduction

The Egyptian type of cotton comprises numerous varieties which have presumably originated by mutation (Kearney, 1914). This presumption is based upon the following facts:

1. Each variety descended from a single individual which differed in several characters from the parent form.
2. The absence or extreme rarity of connecting forms and the infrequency of sterility in both the parental and the mutant stock make it difficult to account for these mutants on the basis of recombination, as ordinarily understood.
3. The new characters of the mutant are uniformly expressed in the successive generations of its offspring as long as hybridization with other forms is excluded.

The observed facts make it difficult to escape the conclusion that these mutants are the result of simultaneous alteration of several factors in the egg cell after fertilization.[1] Otherwise, it is necessary to assume that the mutant has resulted from the union of a male and a female gamete, in both of which similar but independent alteration had taken place with respect to several factors. Probability is so greatly against this interpretation as to make it almost unthinkable.

The question suggests itself, what are the conditions under which mutation occurs in Egyptian cotton? The appearance of mutants has thus far been observed only in mixed stocks (Kearney, 1918, pp. 60–61). Hence, not-

[1] A case of mutation has been thus explained by Hayes and Beinhart (1914).

withstanding the difficulty of interpreting the mutants as direct recombinations, the inference can scarcely be avoided that mutation in this group is conditioned by heterozygosity.

In an endeavor to obtain more definite information on this point it was decided to make simple and back-crossed hybrids between two varieties of Egyptian cotton and to study these hybrids in comparison with line-bred progenies of the parent varieties. Mutants in this group are of comparatively rare occurrence, nothing analogous to the "mass mutation" observed by Bartlett (1915) in *Œnothera* and by De Vries (1918) in *Zea* having been observed. Very large numbers of plants of the hybrid and parental stocks will therefore need to be examined before we may hope to obtain reliable statistics as to the production of mutants. In the meantime, it is believed that what has been learned in regard to the behavior of these hybrids in the first three generations is of sufficient interest to warrant preliminary publication.

Most previous studies of hybrids in the genus *Gossypium* have been made upon interspecific crosses, such as Sea Island cotton (*G. barbadense*) × Upland cotton (*G. hirsutum*) and Egyptian cotton[2] × Upland cotton. In these cases there is very great variability in the F_2 and later generations. Cotton breeders have found it to be practically impossible to "fix" such hybrids, even after selection continued during six or seven generations. On the other hand, little is known of the behavior of crosses between varieties within the same species. Are such hybrids less variable and less difficult to fix by selection, and, if so, can not stable and uniform new varieties be obtained by recombination? It is believed that these questions are partly answered by the data presented in this paper.

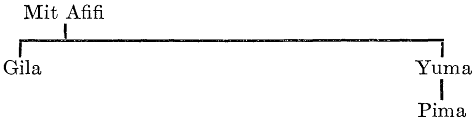
The investigation was conducted at the Cooperative Testing Garden, Sacaton, Arizona, which is conducted

[2] The Egyptian type of cotton, although commonly supposed to be of hybrid origin (Balls, 1912, pp. 3, 4) presents many analogies to a natural species and its differences from American Upland cotton are certainly of specific magnitude.

by the Bureau of Plant Industry in cooperation with the Indian Service. The writers are indebted to Mr. G. N. Collins of the Bureau of Plant Industry for many helpful suggestions throughout the course of the investigation.[3]

Plan of the Investigation

The only varieties of Egyptian cotton of which approximately pure strains were available when the experiment was begun were the Yuma, Gila and Pima varieties, all of which had been developed in Arizona. These varieties were described (with illustrations of the leaves, bracts, and bolls) and an account of their origin was given in an earlier publication (Kearney, 1914). Their relationship may be indicated thus:



The Gila and Pima varieties were chosen because they show the greatest amount of difference in the largest number of characters. Of the three varieties, Gila is most similar to the common ancestor, Mit Afifi, and Pima is the most distinct from it. Gila may, in fact, be regarded as representing a small portion of the area of variation of the extremely heterozygous Mit Afifi stock from which all these varieties have descended, while the characters of Pima are far outside the hitherto observed range of variation in Mit Afifi. The hybrids described in this paper may therefore be taken to represent, in a measure, the result of crossing the mutant Pima with its more remote ancestor, Mit Afifi.

Several typical individuals of each variety were selected in July, 1914. A number of flowers were self-pollinated on each plant and intervarietal cross-pollinations were made among them. The resulting first gen-

[3] It is not practicable to publish in full the voluminous data resulting from this investigation but the writers are prepared to supply, to any one who may be interested, photographic copies of the original records, at the cost of reproduction.

eration parental and hybrid progenies were grown in 1915. Seeds produced by flowers which were selfed on certain individuals in these progenies furnished the second generation, which was grown in 1916. Flowers on selected plants in the second generation parental and F_2 hybrid progenies were again selfed to furnish the third generation parental and the F_3 hybrid progenies, which were grown in 1917.

Some of the flowers on F_1 hybrid plants in 1915 were pollinated from plants in the first generation progenies of the original parent plants of either variety. From the resulting seed 3/4 Pima and 3/4 Gila back-crosses were grown in 1916. Plants were selected in each of the 3/4 back-cross progenies because of their approach to the corresponding predominant parent in respect to important characters. The Pima back-cross plants were pollinated from a plant in the second selfed generation of the Pima parent and the Gila back-cross plants were pollinated from a similar Gila individual. The resulting 7/8 Pima and 7/8 Gila back-cross progenies were grown in 1917.

Every effort was made to grow the various parental and hybrid progenies under as nearly as possible uniform conditions in respect to soil, irrigation and cultural treatment. All comparisons of hybrids and parents have been made on the basis of progenies grown the same season, in order to obviate the influence of different weather conditions. Measurements on the different plants were made, as far as practicable, upon organs which occurred at the same nodes of the axis and branches and which were in the same stage of development. The number of plants on which most of the characters were measured in each generation were, in round numbers:

	F_1 (1915)	F_2 (1916)	F_3 (1917)
Pima	60	200	180
Gila	40	200	100
Pima × Gila	80	400	300

Characters Measured and Significance of the Varietal Differences

The Pima and Gila varieties, as represented by the first and second generation progenies of the selected parent individuals, differed by an amount equal to three or more times the probable error of the difference, in respect to 24 characters. Many of these are physically or physiologically correlated, but six of the characters showed practically no correlation inter se, in either parent. Most of these characters are expressions of size (*e. g.*, the length of the internodes, leaves, floral parts, bolls and fiber) or are ratios between two size characters and expressive of shape. The leaf index $\frac{\text{length}}{\text{width}} \times 100$ and the boll index $\frac{\text{length}}{\text{diameter}} \times 100$ showed especially significant differences between the two varieties named, the difference in the second generation having been 26 times the probable error in respect to leaf index and 46 times the probable error in respect to boll index. In length of fiber the difference between the parents in the second generation was 22 times its probable error. The only characters of diagnostic value which could not be accurately measured and which were therefore determined by grading, were color of the fiber,[4] amount of fuzz on the seeds and roughness of the boll surface (depending upon the depth, number and regularity of distribution of the pits in which the oil glands are situated). Even in respect to these characters the differences were of degree rather than of kind.

The Gila variety, as represented by three successive selfed generations of the progenies of the parent plants, gave larger coefficients of variation for most of the characters than did the Pima variety. Since no general decrease in the variability of either variety was observed after three generations of selfing, it would appear that Gila is inherently more variable than Pima.

The two varieties, as represented by the first and sec-

[4] The two varieties showed no difference in the color of any part of the flower.

ond generation progenies of the plants selected as parents of the hybrids, showed overlapping ranges for all characters excepting fuzziness of the seed and color of the fiber. These two characters were measured on only small numbers and overlapping would very likely have been observed if larger populations had been compared.

The Simple Hybrids

Means

Comparing the means of the simple hybrids (Pima × Gila) with those of the parents, a strong tendency to intermediacy was apparent. The means for a large majority of the characters, in both the F_1 and F_2, lay between the parental means, and in nearly one half of the total number of characters the hybrid means did not differ significantly from the midpoint of the parental means. The relative number of characters for which the departure of the hybrid mean was towards the Pima mean was much greater in the F_1 than in the F_2. This was probably due to increased vigor in the conjugate generation, eight of the thirteen characters which showed a significant[5] departure of the hybrid F_1 mean from the midpoint of the parents being size characters for which the Pima parent gave a larger mean than the Gila parent.

Eleven F_3 progenies of the simple hybrid were grown in 1917 from plants which were selected in the F_2 in 1916 because of their approach to one or the other parent or because of their intermediacy with respect to various characters, especially leaf index and boll index. The F_3 means for these characters in all cases fell between the means of the third generation parental progenies, or else did not differ significantly from the mean of one or the other parent.

Coefficients of Variation

In all three generations the hybrids gave significantly larger coefficients of variation, for most of the characters,

[5] A difference or other quantity is here referred to as "significant" when amounting to three or more times its probable error.

than did the corresponding selfed parental progenies of the Pima variety, but were not significantly more variable than the corresponding Gila progenies. In length of fiber the hybrid F_2 was not significantly more variable than either parent. The hybrid F_2 was significantly more variable than the F_1 in the leaf characters, but not in the boll characters. This result was so surprising that it was accepted only after repeatedly checking the original data. The averages of the coefficients of variation, for leaf index and boll index, of the eleven F_3 hybrid progenies did not differ significantly from the coefficients of the F_2 progeny from which they were derived. The average variability of the F_3 did not exceed that of the third selfed generation of the more variable parent (Gila) and two of the F_3 progenies were not more variable than the corresponding generation of the less variable parent (Pima).

These facts point to the possibility of obtaining a relatively uniform new variety of cotton by hybridization of two varieties belonging to the same general type, although hybrids between different types, such as Egyptian and Upland, are notoriously difficult to fix.[6]

Distributions

The distributions, for the important characters leaf index, boll index and fiber length, of the parental and simple hybrid progenies, are shown in Figs. 1 to 3.

The range of the hybrid F_2 for none of the characters appreciably exceeded the combined parental ranges and for the majority of characters it was more restricted than the latter. The variation was therefore much smaller than in the F_2 of hybrids between less closely related types of cotton, in which the range often greatly exceeds that of both parents. (For example, the Egyp-

[6] Longfield Smith (1915, p. 30) states that hybrids between the not very dissimilar Sea Island and Sakellaridis cottons were "fairly uniform" in the F_2 and F_3. Different behavior was shown by the cross between Sea Island and "St. Croix Native," a type more nearly resembling American Upland cotton. In this case, "new characters, not present in either of the original plants, appear in the first and subsequent generations," and the F_2 and F_3 "split into a mass of types."

tian × Kekchi hybrids described by Cook (1909, p. 12–14) and the Egyptian × Hindi hybrids described by Marshall (1915).)

Little or no evidence of dominance was shown by the distributions, for the various characters, of the F_1 of the

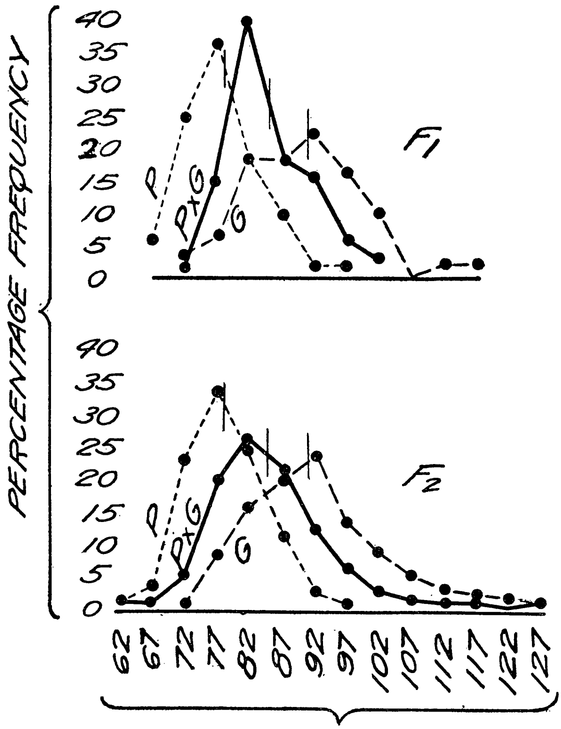


FIG. 1. Leaf index: first and second generation distributions of the parental and simple hybrid progenies. The dotted line curve represents the distribution of the Pima parent, the broken line curve that of the Gila parent and the solid line curve that of the hybrid. The short vertical line on each curve indicates the location of the mean of that population. The figures on the axis of ordinates indicate the number of plants in each class, taken as a percentage of the total number of the population. The figures on the axis of abscissas indicate the classes.

The actual numbers of the respective populations were: F_1, Pima 60, Gila 40, P × G 80; F_2, Pima 213, Gila 203, P × G 418.

simple hybrids. The F_2 distributions were strictly unimodal for all characters excepting the highly variable one length of axis, and even in this case the indication of bimodality was so slight as to be probably insignificant.

No evidence of segregation in definite ratios was obtained.

It is well known that complete dominance in the F_1 and 3:1 segregation in the F_2 are exceptional in size and shape characters such as chiefly distinguished the Pima and Gila varieties of cotton. On the other hand, the question whether the behavior of the Pima $\times$ Gila hy-

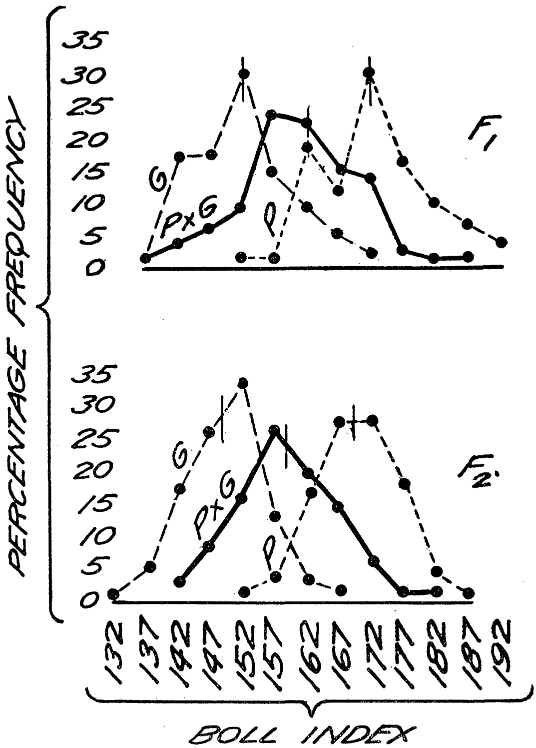


FIG. 2. Boll index: first and second generation distributions of the parental and simple hybrid progenies. Details as in Fig. 1. The actual numbers of the respective populations were: F_1, Pima 60, Gila 40, P $\times$ G 80; F_2, Pima 161, Gila 207, P $\times$ G 419.

brids with respect to such characters might be interpreted by the multiple factor hypothesis is extremely difficult to answer. The differences between the means of the parents for most of the characters, while small, are highly significant, but the parental ranges, in most cases, overlap to such an extent that Mendelian analysis would seem to be out of the question.

A few of the characters in respect to which these varieties differ significantly might be termed "qualitative." These are roughness of the boll surface, color of the fiber and fuzziness of the seed, all of which are included in the lists of allelomorphic pairs of characters in cotton

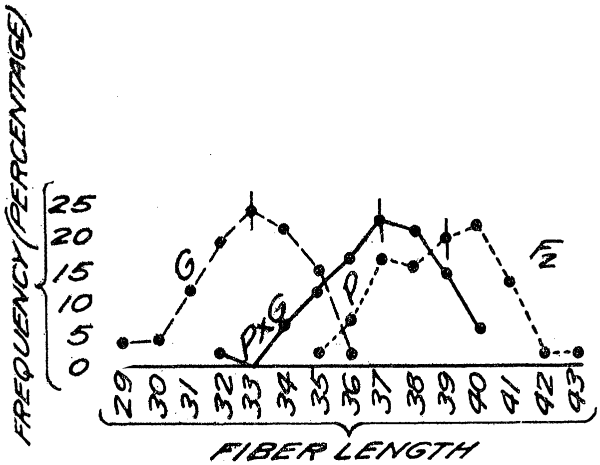


FIG. 3. Fiber length (mm.); second generation distributions of the parental and simple hybrid progenies. Details as in Fig. 1. The actual numbers of the respective populations were: Pima 46, Gila 53, P × G 49.

given by Balls (1909, p. 18) and by McLendon (1912, pp. 168, 169).[7] Yet in the Pima × Gila hybrids these characters behaved like the size and shape characters, showing unimodal distribution in the F_2. It should be noted, however, that in respect to these characters the differences between the two Egyptian varieties are much smaller than the differences between the parents of the wider crosses (Egyptian × Upland and Sea Island × Upland) dealt with by Balls and McLendon. Instead of the differences between pitted and smooth bolls, buff and white fiber and smooth and fuzzy seeds we have, in comparing Pima with Gila, merely the differences between more and less numerously and regularly pitted bolls, lighter and darker buff-colored fiber and more and less fuzz on the seeds.

[7] Complete dominance is apparently a rather rare phenomenon in cotton, even in the case of color characters. It is stated, however, by Leake and Prasad (1914, pp. 126–128) that yellow corolla color and the presence of the petal spot are completely dominant in certain hybrids of Indian cottons.

Correlation of Characters

It was sought to ascertain whether these hybrids show genetic as distinguished from merely physical or physiological correlations, in other words, whether there is coherence in the transmission of the parental characters. To this end, application was made of the test proposed by Collins (1916, p. 439), *i. e.*, comparison of the coefficients of correlation of the F_2 with those of the F_1. It is assumed that if the F_2 coefficient significantly exceeds that of the F_1, in the direction indicated by the relation of the parental means for the two characters, genetic correlation or coherence of characters is indicated. For example, the Pima parent has a lower leaf index and a higher boll index than the Gila parent. If there is coherence of these characters, the hybrid should show a negative correlation and the coefficient of correlation should be significantly larger in the F_2 than in the F_1.

The coefficients of correlation of 40 pairs of characters were determined for both the F_1 (grown in 1915) and F_2 (grown in 1916), upon the basis of one measurement of each character on each plant.[8] In three of these cases the coefficient of correlation of the F_2 was significantly larger than that of the F_1 (difference from 3.5 to 4.5 times its probable error), in the direction indicated by the parental relation. Since, however, the coefficients of correlation of the first generation (1915) and second generation (1916) of the parental progenies had also been found to differ in magnitude, the possibility was considered that the difference in the F_1 and F_2 hybrid coefficients was at least partly due to variations in the weather of the two years. The coefficients of correlation for the three character pairs above mentioned were therefore calculated for a new F_1 which was grown in the same year as the F_2.[9] When the F_2 and the new F_1 coefficients

[8] Two characters of great practical importance and in respect to which the parents differ very significantly, length of fiber and fuzziness of seeds, showed no significant correlations, either with each other or with the leaf and boll characters.

[9] The new F_1 was the result of crosses between daughters of the original parent plants, which had been made in 1915.

were compared, it was found that the former was significantly larger than the latter, in the indicated direction, for only one pair of characters (width of leaf and number of teeth on the involucral bracts) and in this case the difference was only 3.2 times its probable error.[10]

It was sought to throw further light upon this problem by determining the coefficient of correlation in the hybrid upon the basis of progenies rather than of individual plans. The means, for leaf index and boll index, of eleven F_3 hybrid progenies were used for this purpose. These progenies comprised from 8 to 44 plants each and the means were based upon measurement of one leaf and one boll on each plant. Since the Pima parent has the smaller leaf index and the larger boll index, the correlation in the hybrid, if determined by the parental relations of the two characters, should be negative. The coefficient obtained was in fact negative, but was no larger than its probable error ($r = -.17 \pm .18$).[11]

The balance of evidence is therefore strongly against the occurrence of coherence of characters in these hybrids between somewhat closely related, although distinct, varieties of cotton. It does not, of course, follow that the same result would have been obtained in the case of hybrids between less closely related types, especially if these differ in allelomorphic characters rather than in the variable size and shape characters which chiefly distinguished Pima from Gila.[12]

[10] The correlation in question, width of leaf with number of teeth on the involucral bracts, is doubtless physiological, large bracts being associated with large leaves and the number of teeth being greater on the larger bracts.

[11] The existence of an intervarietal correlation by no means implies that the same correlation will be found to obtain within a variety. For example, it is a matter of common observation that most varieties of cotton which have very long fiber have relatively sparse fiber, and vice versa. But when the correlation between fiber length and lint index (weight of fiber per 100 seeds) was plotted for 80 plants of the Pima variety, the value of r was found to be only $.07 \times .07$, showing the complete absence of an intravarietal correlation.

[12] Instances of coherence of characters in hybrids of Egyptian with Upland cotton have been reported by Cook (1909, pp. 16, 17 and 1913, p. 53). On the other hand, Marshall (1915, pp. 57, 61), describing the F_2 of hybrids

THE BACK-CROSSED HYBRIDS

The means of the $\frac{3}{4}$ back-crossed hybrids for nearly all characters showed departures from the midpoint of the parental means which were both significant and towards the mean of the respective preponderant parent (Pima or Gila). In the $\frac{7}{8}$ back-crosses, the mean virtually coincided with those of the preponderant parent, as the following data show:

Progeny Means of:	Leaf Index	Boll Index
Pima	78.1 ± .14	173 ± .18
Pima $\frac{7}{8}$ back-cross [(P × G) × P] × P	78.7 ± .63	179 ± .66
Gila $\frac{7}{8}$ back-cross [(P × G) × G] × G	94.1 ± .47	153 ± .90
Gila	93.1 ± .47	156 ± .51

The distributions, for leaf index and boll index, of the Pima $\frac{7}{8}$ back-cross, were embraced by those of Pima and the distributions of the Gila $\frac{7}{8}$ back-cross were embraced by those of Gila. It is therefore apparent that twice back-crossing the simple hybrid with either of its parents has sufficed to eliminate the influence of the other parent in the expression of these characters.

ABSENCE OF MUTANTS

Careful examination, in 1916, of every plant in the F_2 progenies of the simple hybrids and in the $\frac{3}{4}$ back-cross progenies, showed only various recombinations of the Pima and Gila characters. A large majority of the simple hybrid plants were approximately intermediate, although occasional individuals showed a near approach to one or the other parent. Most of the back-cross plants, as compared with the simple hybrid individuals, showed clearly the preponderating influence of the $\frac{3}{4}$ parent, but few if any plants in the $\frac{3}{4}$ back-cross progenies could have been classed as wholly Pima or wholly Gila, the influence of the one-quarter parent being observable in the great majority of cases. No instance of

between the equally different Egyptian and Hindi cottons, states: ''Nor was it possible to discover any general correlations or definite associations between any of the more important structural differences.''

the occurrence of new or extra-parental characters was detected, although a few plants in the F_2 of the simple hybrid slightly exceeded the range of one or the other parent. Examination, in 1917, of the F_3 progenies of the simple hybrids, and of the 7/8 back-cross progenies also failed to reveal the occurrence of any extra-parental characters. Nor have any new characters been detected in the first, second or third generation progenies from selfed seed of the parent individuals. It is evident, therefore, that nothing in the nature of a mutant has yet appeared in any of these line-bred and hybrid stocks.

It was not, however, expected that mutants would be detected in these small progenies, which were grown for the purpose of studying, under controlled conditions, the behavior of the hybrids in the earlier generations and to provide seed for the growing of each stock on a more extensive scale. Statistical evidence regarding the production of mutants can scarcely be expected until much larger numbers of plants have been examined. The stocks resulting from repeated back-crossing should be especially interesting to study in regard to the occurrence of mutation.[13]

CONCLUSION

The investigation here described was undertaken in the endeavor to ascertain the conditions under which mutants are produced, in Egyptian cotton. Simple and back-crossed hybrids were made between two varieties (Pima and Gila) which differ significantly in numerous characters. Three generations of the hybrid progenies and of progenies from selfed seed of the parent individuals, were grown. No evidence of the appearance of

[13] "Variations toward Upland or Hindi characters arising in dilute hybrid stocks of Egyptian cotton have been found to yield progenies with more stable expression of characters than direct hybrids between Egyptian and Upland cotton. Such facts suggest the possibility of developing a new method of breeding by dilute hybridization. By the use of a small proportion of foreign blood as a means of inducing mutative variations in otherwise uniform stocks it may be possible to secure desired combinations of characters in more stable form than they can be obtained by direct hybridization." (Cook, 1913, p. 96.)

new characters was detected in any of these progenies, but since mutants in Egyptian cotton are comparatively rare, it will doubtless be necessary to examine much larger populations before definite conclusions can be drawn as to the occurrence of mutation in these stocks.

The principal interest of the data thus far obtained attaches to the behavior of hybrids between varieties belonging to the same general type, as compared with that of the hybrids between different species of *Gossypium*, which have hitherto been the principal subject of genetic investigation in this group of plants.

The varieties used in this investigation are distinguished chiefly by size and shape characters, although a few of the characters in which they differ significantly have been found to behave as allelomorphs in hybrids between less nearly related forms of *Gossypium*. The Pima $\times$ Gila hybrids, however, showed no evidence of segregation in definite ratios in respect to any of the characters measured. There was little or no evidence of dominance in the F_1, and the F_2 distributions were practically without exception unimodal. The means of the simple hybrid were in most cases intermediate between those of the parents. The result of twice back-crossing the simple hybrid upon either parent was to obliterate the expression of the characters of the other parent.

It could not be demonstrated that genetic correlation or coherence of characters occurs in these hybrids. Apparently all characters which are not correlated physically or physiologically are transmitted independently.

The second and third generations of the hybrids, as compared with the parents after two and three generations of selfing, were not more variable than Gila, and were only a little more variable than Pima. This fact is of practical importance in cotton breeding, since it points to the possibility of obtaining relatively stable and uniform recombinations of the desirable characters of varieties belonging to the same general type, although breeders have found this to be well nigh impossible in

wider crosses such as those of Egyptian (or Sea Island) with Upland cotton.

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